

APPENDIX H

AN APPROACH TO POPULATION VIABILITY ANALYSIS FOR STEELHEAD AND SALMON USING STOCK-RECRUITMENT CURVES WITH MULTIPLE LIFE STAGES

*Dan Rawding
Washington Department of Fish and Wildlife*

Overview

The results from Appendix G suggest that fitting recruitment curves to adult recruits per spawner data is unlikely to provide precise estimates of intrinsic productivity for salmon populations that could be used for viability criteria. This may be due to measurement error, environmental variation within the data, and/or the addition of hatchery spawners to naturally spawning populations so that few populations have low enough spawning escapements to accurately measure intrinsic productivity. However, precision in estimating intrinsic productivity may potentially be increased by partitioning the life cycle into freshwater and marine phases. This appendix explores an approach to setting viability criteria in which density dependence is assumed to occur in the freshwater life stage, and marine survival is considered a density-independent factor driven by the environment. Criteria with this approach would likely be a demonstration that, based on the assumption that habitat in the freshwater environment is stable, a population has sufficient freshwater productivity and capacity to persist in the face of hypothesized future marine survival patterns. With this approach, there is no single freshwater productivity, and capacity target, as multiple combinations of productivity and capacity, could produce identical extinction risks. Instead of a single *a priori* target, the approach could potentially be used retrospectively to evaluate whether a population has improved such that it has an acceptably high probability of persistence.

The approach in this appendix is applied to evaluate the current status of the Wind River steelhead population. Model parameters were fitted using the Wind River data, and a forward project of abundance was modeled under a number of hypothesized future ocean survival patterns. The Wind River data have not yet been analyzed using a formal model selection procedure like that described in Appendix G. There is concern about the level of applicability of this for this approach because few populations in the Willamette-Lower Columbia (WLC) domain have intensive smolt monitoring programs. Also, the Wind River data set is very short, and some WLC Technical Recovery Team (TRT) members are concerned that apparently better fit of the multiple life-stage models may be an artifact of simply adding another parameter (additional parameters almost always lead to better fit, but may not actually contribute to the utility of the model). However, the approach is promising. Assuming the appropriate data are collected and robust predictions can be made about future patterns of marine survival and

freshwater habitat, the approach provides a potential alternative to the population change criteria approach.

The Model

This approach uses a spawner-recruit relationship (SRR) to assess extinction risk (Chilcote 1998, Chilcote 1999, Routledge and Irvine 1999, and Johnson et al. 2000). Salmonids often demonstrate Ricker, Beverton-Holt, and/or hockey-stick SRR relationships. These SRR relationships assume density-independent mortality; that is, at low spawning densities, survival is independent of stock size (Hilborn and Walters 1992). However, it is unlikely that a population can continue a high rate of reproduction as the stock continues to increase. Eventually, available resources limit populations, and some reduction of recruits per spawner is observed as the spawning stock size increases. The Beverton-Holt and hockey-stick models assume that the quality and quantity of freshwater spawning and rearing habitat limits freshwater production of juvenile salmonids (Beverton and Holt 1957, Barrowman 2000). Unlike the Beverton-Holt and hockey-stick models, the Ricker model assumes declining recruitment at higher stock sizes. For the freshwater relationship the SRR can take any one of these forms, but for simplicity this overview will work with the Beverton-Holt form. The Beverton-Holt model is fit to the spawner and smolt data using maximum likelihood methods and assuming lognormal error (Hilborn and Walters 1992). As smolts enter the marine environment I assumed they had density-dependent survival (Ward 2000, Johnson et al. 2000, Emlen et al. 1990). Pearcy (1992) summarized data for anadromous fish that suggested the variation in marine survival often exceeds the variation in freshwater survival. Cramer (1996) confirmed that considerable variation is in the marine environment by examining hatchery coho and chinook salmon returns. This combination of density dependence in freshwater and density independence in the marine environment can be expressed in a stock-recruitment equation using a Beverton-Holt model as:

$$R = (\alpha S / (1 + \alpha S/\beta)) * m \quad (1)$$

where

R= the number of adults,
S = the number of spawners,
 α = the freshwater intrinsic productivity of the stock,
 β = the freshwater carrying capacity of the stock, and
m= marine survival.

Since steelhead are iteroparus, another term was added to account for repeat spawners. In SRR analysis, it is often assumed that environmental factors are constant over time. However, conditions such as floods during incubation and summer low flow have all been shown to alter the survival of a cohort. To account for this environmental variation, another term was added to the SRR, where e^{ϵ_t} was drawn from a normal distribution, $N(0, \sigma)$. The final added term is to ensure that the random error has a mean of 1.

$$R = (\alpha S / (1 + \alpha S/\beta)) * m * c(S_{t-1}) * e^{\epsilon_t} * e^{-(\sigma^2/2)} \quad (2)$$

where

- S_{t-1} = spawners from the previous year,
- ϕ = the repeat spawner rate,
- e_t = a normally distributed variable with a mean of zero,
- $(\sigma^2/2)$ = process error of the model fit.

These equations are incorporated into an age structure model using freshwater and ocean-age steelhead data from the Wind River. This approach incorporates realistic levels of parameter uncertainty in the freshwater and marine environments. If the smolt production is not limited under favorable ocean conditions, smolt production can be unrealistic. Therefore, an upper bound on smolt production was needed. For the Beverton-Holt model, I chose to limit production to 1.5 times the capacity. This has a limited effect on extinction risk since extinction would most likely occur under poor ocean conditions in which the predicted smolt production would not be capped.

I initiated the age-structure model at 500 spawners, the recent mean escapement. The simulations ran for 100-plus years. To estimate extinction risk I recorded the lowest population size, then recorded the number of times the population dropped below a quasi-extinction threshold. Chilcote (1999) suggested a quasi-extinction threshold of 150 spawners for small steelhead populations and 300 for larger steelhead populations. McElhany (2002) suggests quasi-extinction thresholds of 50. Based on the results of 100 simulations the extinction risk is estimated to be the percentage of time a population dropped below each quasi-extinction threshold. Alternative expressions can be adapted for the hockey-stick and Ricker models.

The underlying approach for pursuing life-cycle SSR modeling is that some of the variation in population abundance can be explained by fluctuations in run size and changes in marine survival. Figures H.1 and H.2 demonstrate why this may be true for the WLC domain. The data for Trout Creek steelhead demonstrate that smolt abundance is related to the abundance of female spawners (Figure H.1). The Kalama River data show strong correlation between steelhead run size and smolt-to-adult survival (Figure H.2). Since the goal of this approach is to estimate population persistence, future estimates of marine survival must be incorporated into the model. Five approaches were considered for capturing the future variation in marine survival. The first is that marine survival is random and does not follow a pattern. However, salmon populations have been documented to have periods of higher and lower productivity (Mantua et al. 1997). Anderson (1998) documented these periods for the catch of Columbia River chinook salmon. Due to the change in productivity over decadal scales, it is unlikely that random variation is likely occurring, and this option was not pursued.

The second approach was that marine survival followed a step function, with periods of poor ocean productivity followed by periods of favorable ocean productivity. Hare (1999) indicated this phase shift worked well for explaining the variation in Bristol Bay sockeye salmon SRR. In the productive period the intrinsic productivity on these sockeye stocks was twice that measured during the unproductive periods. However, in a poor or favorable marine survival pattern there is variation. To account for this, I set the variation to randomly range from the lowest to half of the high plus low during the poor period to the highest to half high plus low during the favorable period. Future ranges of marine survival were generated by randomly generating survivals within this range.

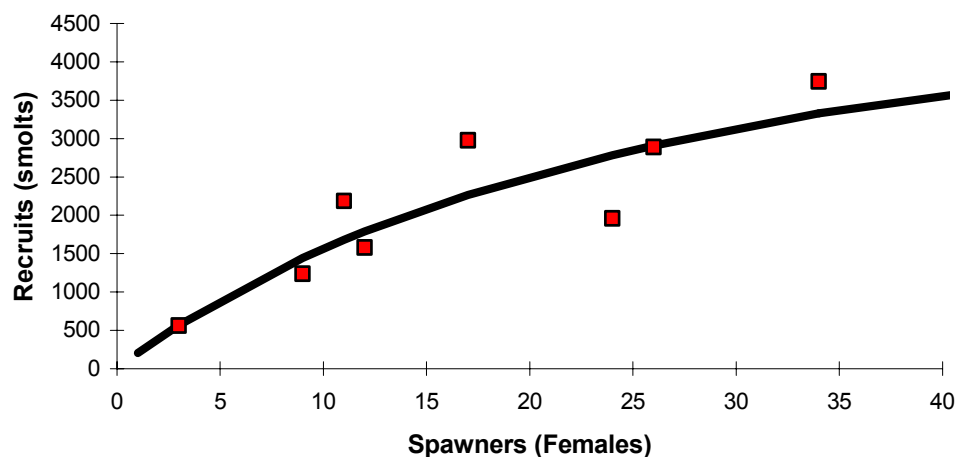


Figure H.1 Beverton-Holt model fit to wild steelhead data on Trout Creek, a tributary to the Wind River. This demonstrates that much of the variation in smolt abundance is explained by the number of spawners.

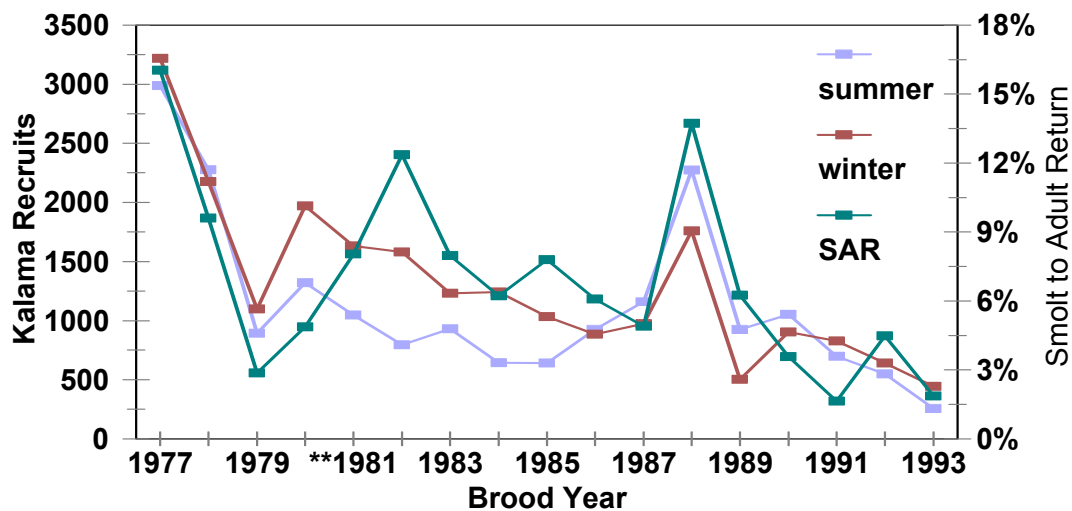


Figure H.2 Correlation Kalama River wild steelhead returns and hatchery smolt-to-adult survival rates in the Kalama River. The increase in the 1981 and 1982 broodyears SAR (smolt-to-adult return) was due to increased straying of Cowlitz and Toutle hatchery steelhead into the Kalama River.

The third approach was to use the Pacific Decadal Oscillation (PDO) as a surrogate for marine survival. The lowest observed smolt-to-adult survival was set to the annual PDO estimate that was the lowest, and the highest marine survival was set to the highest annual PDO. The simulation assumed the PDO repeated itself every 100 years. While strong correlations have been exhibited with the PDO for some salmonids, flows and hydroelectric operations in the Columbia River and local estuarine conditions may have a strong influence on survival as well.

A fourth approach was to use a sine wave to simulate cycles in ocean productivity. Hare et al. (1999) suggested that ocean cycles are decadal, and the PDO had a period of approximately 25 years. I calculated the highest and lowest observed smolt-to-adult survival, added the high and low, and divided by 2 to estimate the mean. The period on the sine wave was the mean minus the low.

Salmon populations face a higher level of extinction risk during periods of low ocean productivity. The most conservative approach was to set the future smolt-to-adult survival to the lowest observed in the data set.

Results

A Beverton-Holt model was fit to the Wind River steelhead SRR data (Figure H.3) Due to small sample size ($n = 8$) for Wind River steelhead, the original data point in the series was not included because there was uncertainty in the smolt-trapping data (the trap was out from April 22–May 5 due to damages from a flood), and the intrinsic productivity fit with all eight points led to a potentially unrealistic range observed for this species. However, I used all eight points to estimate σ . The most conservative estimate of smolt-to-adult survival for Wind River steelhead was 0.8%. In all simulations this led to a population of 0 fish in about 100 years (Figure H.4). Under this scenario, the probability of population persistence was 0%. When marine survivals were fixed at less than 1.2%, the population was likely to be less than the quasi-extinction threshold of 50 spawners (Figure H.5). The sine wave results indicate that when the smolt-to-adult survival ranges from 0.8% to 6% the probability of dropping below 50 adults is low. More simulations are needed to fully develop this criterion.

Discussion

A critical assumption of this or any population viability analysis (PVA) is stationarity; that is, that the environment in which the past data was collected is the same or very similar to the future condition being modelled. If this is not the case, there is no scientific basis for predicting future population sizes, unless one can accurately describe the future environment used by salmon and the new relationship between salmon and their future environment. Salmon abundance and productivity are correlated to freshwater, estuarine, and ocean habitat.

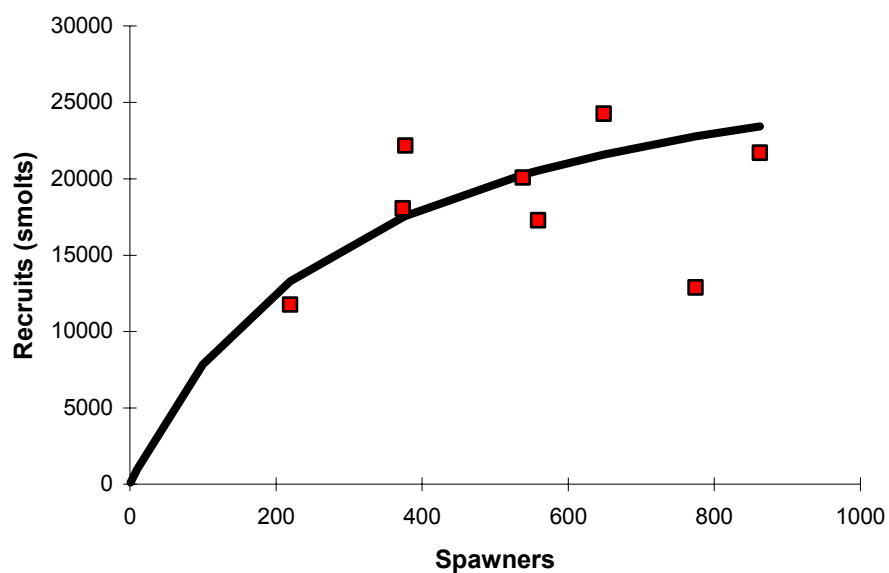


Figure H.3 A Beverton-Holt fit for Wind River steelhead, broodyears 1994–2000.

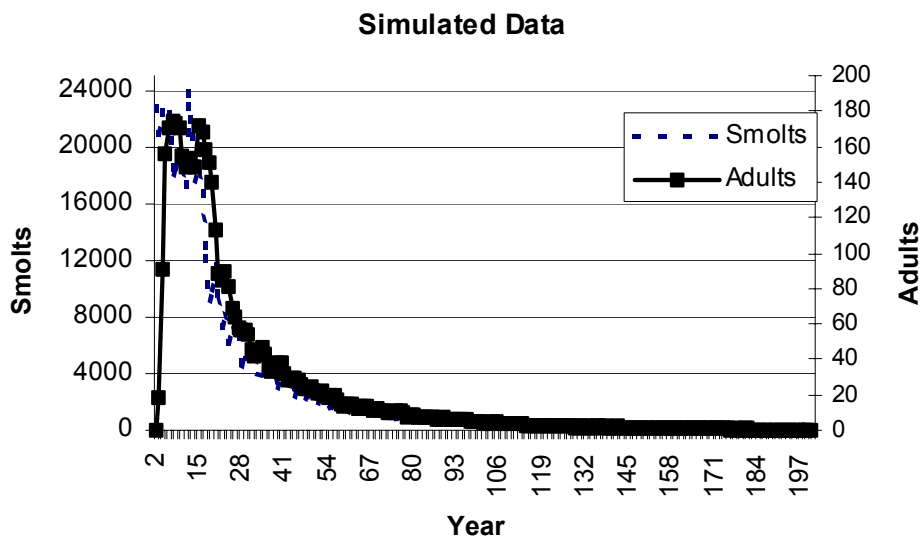


Figure H.4 Abundance of Wind River steelhead adults and smolts under lowest marine survival (0.8%). Modeling projects 0 adults in 100 years.

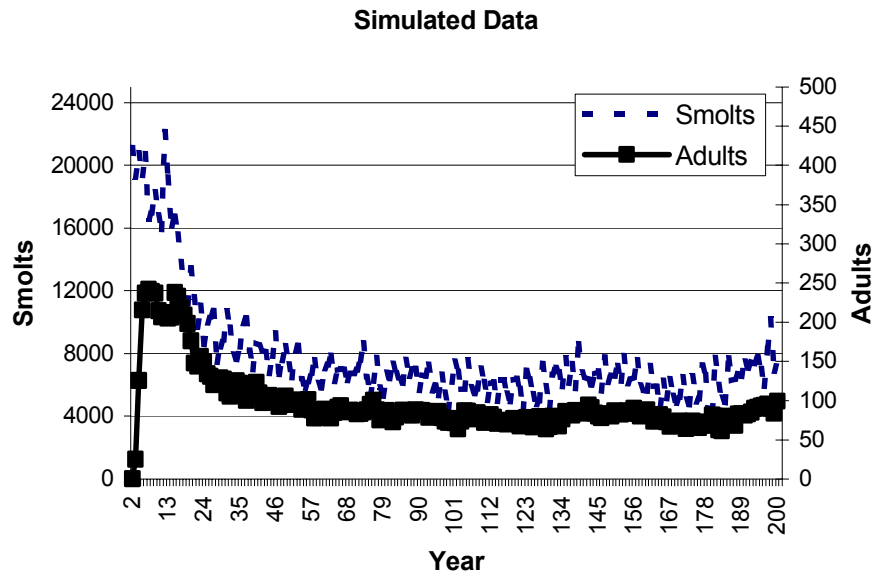


Figure H.5 Abundance of Wind River steelhead adults and smolts under a marine survival of 1.2%. The lowest estimated population size was 64 adults.

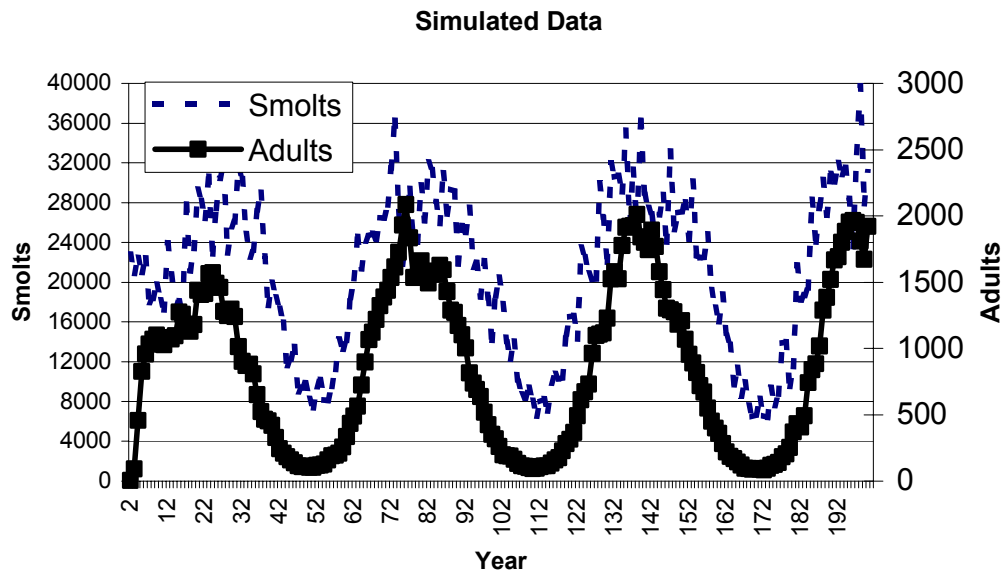


Figure H.6 Abundance of Wind River steelhead adults and smolts under 60-year ocean cycle with lowest marine survival (0.8%) and highest. Model predicts the minimum abundance will be 69 spawners.

Understanding how habitat is likely to change and the fish's response to this change would improve the predictability of any PVA. For this PVA to be successful, salmon habitat over the measuring period and over the forecast period must be consistent, there must be "no net loss in habitat." Furthermore, the range in ocean productivity over the measurement period must accurately reflect the future (i.e., no global warming). Therefore, to ensure that any PVA modeling is forecasting correctly, there must be an adequate assessment of existing habitat regulations to ensure stationarity into the future. Without this constant freshwater habitat the predictive ability of all PVA modeling is called into question.

The quasi-extinction threshold is very important because all PVA are very sensitive to this parameter. The concept of a quasi-extinction threshold can be simply stated: When a population drops below this level the chance for extinction is very high due to loss of genetic diversity, the ability to find a mate, and increased catastrophic risk. McElhany (2002) identified 50 spawners as the quasi-extinction threshold. However, a population that persists at 50 spawners for long periods of time will be at increased extinction risk due an erosion of genetic diversity.

Another parameter that PVA models are sensitive to is the intrinsic productivity or productivity at low spawning densities. If, at low densities, populations can produce many recruits, they show resiliency. Populations with high resiliency have a higher probability of persistence than populations with lower resiliency. However, Appendix E indicates that this parameter may be difficult to estimate unless a life-cycle approach is used. The data required for life-cycle modeling are not usually collected in current salmon or steelhead population monitoring programs.

The utility of PVA models is increased if they provide a constant target, determine population status prior to listing, provide information that assists in identifying factors for decline, and assess individual or a suite of actions in a recovery plan. This approach tries to address these concerns. When the various biological review teams (BRTs) recommended to list chinook, chum, and steelhead within the Lower Columbia River domain, there was considerable disagreement about whether populations should be listed, and whether they should be listed as threatened or endangered under the Endangered Species Act (ESA). There was no quantitative analysis of individual populations regarding their viability, which was appropriate since the BRT was concerned with assessing evolutionarily significant unit (ESU) risk. Given the range of professional opinions among the BRT members, it is likely that some populations within the ESU were healthy at the time of listing. Therefore, the PVA model should not make *a priori* assumptions about population status—that all populations need to grow to be viable. The model should independently assess the population's status without knowing how other models assessed its status. This approach is important because it then becomes a tool for assessing the status of a population for a listing decision.

This type of PVA was in direct response to comments received from the first draft. The Wind River data were included as an example of an alternative approach to the population change criteria (McElhany 2002). The Wind River data set is not of sufficient duration to fully estimate extinction risk. In addition, data points higher and lower than the eight observed would better define the freshwater relationship over a broader range of conditions. Data sets that encompass 20 years if they cover the range in environmental conditions should be considered in this or similar PVA approaches.

References

- Anderson, J. J. 1998. Decadal climate cycles and declining Columbia River salmon. *In*: Sustainable fisheries conference proceedings.
- Barrowman, N. J., and R. A. Myers. 2000. Still more spawner-recruit curves: The hockeystick and its generalizations. *Can. J. Fish. Aquat. Sci.* 57: 665–76.
- Beamish, R. J., D. J. Noakes, et al. 1999. The regime concept and natural trends in the production of Pacific salmon. *Can. J. Fish. Aquat. Sci.* 56: 516–26.
- Beverton, R. J., and S. J. Holt. 1957. On the dynamics of exploited fish populations. U.K. Min. Agric. Fish., Fish. Invest. (Ser. 2) 19, 533 p.
- Chilcote, M. 1998. Conservation status of steelhead in Oregon. Ore. Dept. of Fish and Wildlife, Portland, Ore. 108 p.
- Cramer, S. P. 1998. The effect of environmentally driven variation in recruitment and sustainable yield from salmon populations. Sustainable fisheries conference proceedings.
- Emlen, J. M., R. R. Reisenbichler, A. M. McGie, and T. E. Nickelson. 1990. Density-dependence at sea for coho salmon. *Can. J. Fish. Aquat. Sci.* 47: 17465–17472.
- Hare, S. R., N. J. Mantua, et al. 1999. Inverse production regimes: Alaska and west coast Pacific salmon. *Fisheries* 24: 6–14.
- Hilborn, R., and C. Walters. 1992. Quantitative fisheries stock assessment: Choice, dynamics, and uncertainty. Chapman and Hall, New York. 570 p.
- Johnson, N. T., E. A. Parkinson, A. F. Tautz, and B. R. Ward. Biological reference points for conservation and management of steelhead. *Can. Stock Assess. Secr. #* 2002/126.
- Mantua, N. J., and S. R. Hare, et al. 1997. A Pacific interdecadal climate oscillation with impacts on salmon production. *Bull. Am. Meteorol. Soc.* 78: 1069–79.
- McElhany, P. 2002. Demographic modeling and population change criteria.
- Pearcy, W. G. 1992. Ocean ecology of North Pacific salmonids. University of Washington Press, Seattle.
- Routledge, R. D., and J. R. Irvine. 1999. Chance fluctuations and survival of small salmon stocks. *Can. J. Fish. Aquat. Sci.* 56: 1512–1519.

Ward, B. 2000. Declivity in steelhead recruitment at the Keogh River over the last decade. Can. J. Fish. Aquat. Sci. 57: 298–306.